

Supplementary Information

Population dynamics and the evolution of cooperation in group-structured populations

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In this supplementary text, we give a more detailed discussion of our model and the group-growth mechanism. Furthermore we show comparisons of our analysis with experiments by Chuang et al. [1].

1 The Model

Here, we give details on the consecutive steps of the "life-cycle" of the meta-population. We first specify the group formation step before considering the dynamics within groups (group evolution step).

1.1 The Group Formation Step

Starting with an initial fraction of cooperators x_0 in the population, M groups are formed. Both, group size and group composition, are randomly distributed. Each group $i \in [1, M]$ initially consists of $\nu_{0,i}$ individuals. If the population from which the groups are formed

is much larger than Mn_0 , $\nu_{0,i}$ follows a Poisson distribution¹,

$$P(\nu_{0,i}) = \frac{n_0^{\nu_{0,i}}}{\nu_{0,i}!} \exp(-n_0), \quad (\text{S1})$$

with mean n_0 . Further, the initial composition of each group is also formed randomly. The probability for $\zeta_{0,i}$ cooperators in a group i is assumed to be given by a Binomial distribution

$$P(\zeta_{0,i}) = \binom{\nu_{0,i}}{\zeta_{0,i}} x_0^{\zeta_{0,i}} (1 - x_0)^{\nu_{0,i} - \zeta_{0,i}} \quad (\text{S2})$$

with mean $x_0\nu_{0,i}$. The initial fraction of cooperators $\xi_{0,i}$ within each group is thereby given by $\xi_{0,i} = \frac{\zeta_{0,i}}{\nu_{0,i}}$.

By this we assume the groups to be formed at random without any bias. This corresponds to a worst case scenario for cooperators which gain no additional advantage due to positive assortment. Note, that the same initial distribution of group compositions is reached if one assumes both, the initial number of cooperators (C) and free-riders (F), to be Poisson distributed with mean values λ_C and λ_F , respectively. The mean values are related by $n_0 = \lambda_C + \lambda_F$ and $x_0 = \lambda_C / (\lambda_C + \lambda_F)$.

1.2 The Group Evolution Step

After the groups were formed randomly, they grow and evolve separately. In the following, we consider the dynamics within one specific group i in detail. As emphasized in the main text, we include two essential requirements experiments on microbial systems have in common. First, in each group cooperators (C) grow slower than free-riders (F). Second, groups with a higher fraction of cooperators grow faster and are bounded by a higher maximum group size (carrying capacity) than groups with a lower one. To account for these facts, the growth rates have to consist of a group related and a trait/type specific

¹This holds for typical conditions of small population bottlenecks as observed in bacterial life-cycles.

part [2, 3]. We, therefore, denote the per capita growth rate of an individual of type $S \in \{C, F\}$ within group i as

$$G_S(\xi_i) = g(\xi_i) \frac{f_S(\xi_i)}{\langle f \rangle}, \quad (\text{S3})$$

where $g(\xi_i)$ is the group related, $f_S(\xi_i)$, $S \in \{C, F\}$ is the species related part, and $\langle f \rangle = \xi_i f_C(\xi_i) + (1 - \xi_i) f_F(\xi_i)$ is the average fitness. The normalization of the fitness, $f_S(\xi_i)/\langle f \rangle$, is a convenient choice to disentangle the influence of global and relative parts more easily. Further, the group related part, $g(\xi_i)$, which accounts for the growth advantage of more cooperative groups, is assumed to increase linearly with ξ_i . For specificity, we use experimental conditions similar to those presented in reference [1, 4]. In these experiments, a purely cooperating population growth to an about ten times higher population size than a purely defecting one. In our model, the maximum population size scales with g and therefore we set

$$g(\xi_i) = r(1 + p\xi_i). \quad (\text{S4})$$

Here r determines the overall time scale for growth and defines our units of time, i.e. it is set to one unless specified otherwise. In the main text we have used $p = 10$ for specificity; see also section 3 where we compare with the experimental data by Chuang et al. [1].

Note, however, that the qualitative findings, especially both evolutionary mechanisms, do not depend on the exact form of $g(\xi_i)$ but only on the fact that $g(\xi_i)$ is monotonically increasing with the fraction of cooperators. The trait specific part, $f_S(\xi_i)$, includes the different growth rates of cooperators and free-riders within group i . We here employ the standard formulation of evolutionary game theory and assume it to be given by the payoff matrix of a Prisoner's dilemma game [5, 6]. The trait specific parts are given by

$$\begin{aligned} f_C(\xi_i) &= 1 + s[b\xi_i - c], \\ f_F(\xi_i) &= 1 + sb\xi_i, \end{aligned} \quad (\text{S5})$$

and the fitness advantage of free-riders $\Delta f = f_F(x) - f_C(x) = -sc$ is frequency independent. For specificity, we set $b = 3$ and $c = 1$. Thereby, the selection strength s is the only free parameter controlling the fitness difference, Δf , which corresponds to the advantage of free-riders within each group. In the experiments [1, 4], the selection strength was of the order $s \sim 0.05$. In our manuscript, we set $s = 0.1$ as an upper approximation of this value.

To model growth bounded by restricted resources we further introduce per capita death rates which increase linearly with the number of individuals in a group,

$$D_S(\nu_i) = \frac{\nu_i}{K}. \quad (\text{S6})$$

These are independent of the specific type S and lead to logistic-like growth within each group. K sets the scale of the maximum group size [7]. In detail, for purely defecting groups the carrying capacity is K while it is $(1+10)K$ for purely cooperating ones. For the discussed results, only the ratio of group sizes and not their absolute values are important. Hence, for numerical convenience, we set K to a constant value, $K = 100$.

The full stochastic dynamics follows a master equation which can be derived by the per capita growth and death rates, Eqs. (S3) and (S6). This master equation gives the temporal evolution of $P(\xi_i; \nu_i; t)$, the probability for group i to consist of ν_i individuals with a fraction of ξ_i cooperators at time t . We use the Gillespie algorithm to perform stochastic simulations [8].

While fluctuations strongly affect the dynamics, it is still instructive to look at the deterministic description where fluctuations during the group-evolution step are neglected. This deterministic dynamics within each group, i , is then given by rate equations for the

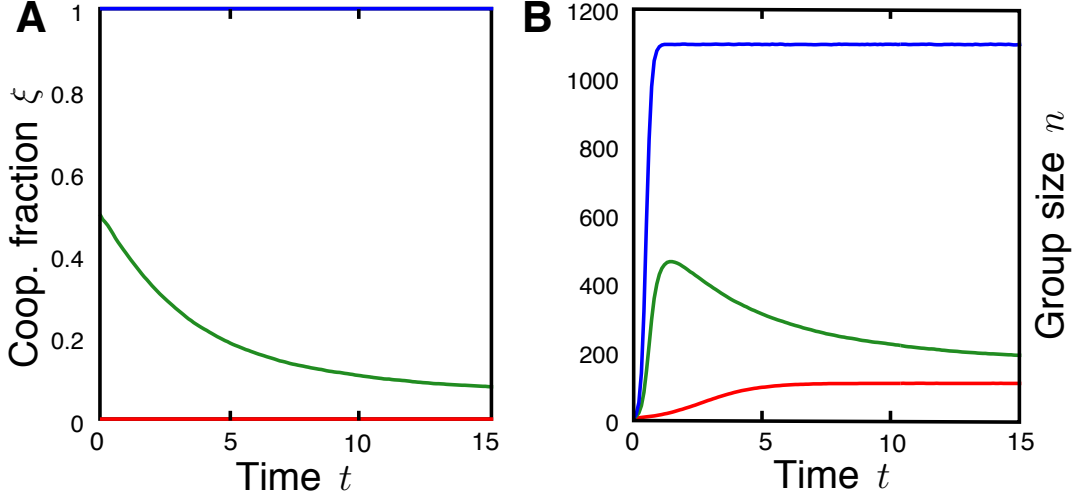


Figure S1: Dynamics in single groups. **A** Evolution of cooperation. For a mixed group (green), the fraction of cooperators declines due to the fitness advantage of free-riders while it stays constant for purely cooperating (blue) or defecting (red) groups. **B** Logistic like growth of the group size. For pure groups, the group-related advantage of more cooperative groups is most visible. Purely cooperating groups (blue) grow faster and reach a larger maximum carrying capacity than groups of only free-riders (red). A mixed group (green) grows faster than a group of only free-riders at the beginning. However also in the initially mixed group only free-riders can remain in the long run, and the carrying capacities of both groups become the same. The simulation average over different realizations of only one group. Parameters are $n_0 = 6$ and $s = 0.1$, ξ_0 is equal to 0 (red), 0.5 (green), and 1 (blue).

fraction of cooperators ξ_i and the total group size ν_i :

$$\begin{aligned}\partial_t \xi_i &= -s(1 + 10\xi_i)\xi_i(1 - \xi_i), \\ \partial_t \nu_i &= (1 + 10\xi_i - \nu_i/K)\nu_i.\end{aligned}\tag{S7}$$

Thus, in a deterministic manner, intra-group evolution is described by a replicator-like dynamics while the size of each group follows logistic growth (with a ξ_i dependent growth rate and carrying capacity). We illustrate this dynamics in Fig. SS1 for three different initial conditions.

Table S1: Per capita growth rates of cooperators and free-riders in two groups

	group 1	group 2
fraction of cooperators ξ_i	3/4	1/4
per capita growth rate cooperators, $g(\xi_i)f_C(\xi_i)/\langle f \rangle$	8.31	3.33
per capita growth rate free-riders, $g(\xi_i)f_F(\xi_i)/\langle f \rangle$	9.05	3.58

Two groups, $i = 1$ and $i = 2$ in comparison. While the per capita growth rates of cooperators are smaller than the per capita growth rates of free-riders within every group, the per capita growth rate of cooperators in the more cooperative group 1 strongly exceeds the per capita growth rate of free-riders in the less cooperative group 2 due to the group related fitness $g(\xi_i)$. The strength of selection is given by $s = 0.1$.

2 The Group-Growth Mechanism

As stated in the main text, the group-growth mechanism relies on the faster growth of more cooperative groups. Even though cooperators reproduce slower compared to free-riders in the same group, the positive effect on group-growth can outbalance this disadvantage. For an illustration, see the specific example given in Table S1.

Here, we quantify the growth advantage of more cooperative groups. For this, we consider only short times $t \ll 1/s$. Then, and in the limit of weak selection, $s \ll 1$, the deterministic time evolution, given by Eqs. (S7), is

$$\begin{aligned}\xi_i &= \xi_{0,i} \\ \nu_i &= \nu_{0,i} \exp [g(\xi_{0,i})t].\end{aligned}$$

The overall fraction of cooperators can be calculated by averaging over all possible initial group compositions,

$$x(t) = \frac{\sum_i P(\xi_{0,i}; \nu_{0,i}) \xi_i \nu_i}{\sum_i P(\xi_{0,i}; \nu_{0,i}) \nu_i}.$$

By differentiating with respect to time t , we find the following expression

$$\frac{d}{dt}x = \text{Cov}(x, g(x)). \quad (\text{S8})$$

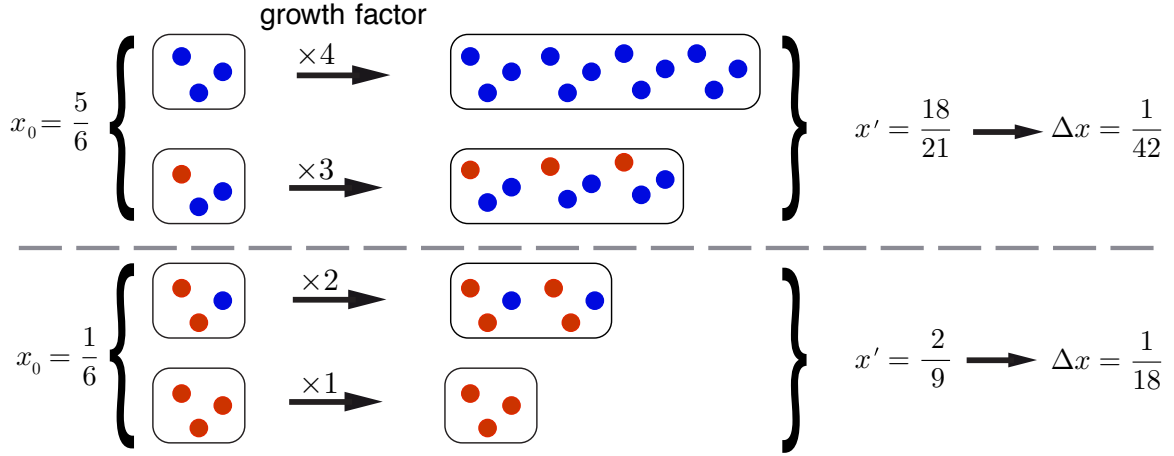


Figure S2: How the group-growth mechanism depends on the fraction of cooperators. Two sets of two groups are compared, one with a low fraction of cooperators (bottom) and one with a high one (top). Both groups evolve for a certain time, here with $g \propto 1 + 3x$ and no selection advantage for free-riders, $s = 0$. As can be readily seen, the change in the fraction of cooperators is larger for groups with a smaller initial fraction of cooperators.

This corresponds to a Price equation on the group level [9, 10], here stating that an increase in the fraction of cooperators is possible in principle if there is a positive correlation between x and the group related growth $g(x)$. However, for longer times $t > 1/s$ the selection advantage of free-riders counteracts the group-growth mechanism such that it can only act transiently.

As shown in the main text, the strength of the group-growth mechanism depends strongly on the initial fraction of cooperators. This is illustrated in Fig. SS2.

3 Comparison with experiments on synthetic microbial system by Chuang, Rivoire and Leibler

We have compared our theoretical analysis with recent experiments by Chuang et al. [1] on a synthetic microbial model system. They have studied regrouping populations with initial population size n_0 in the range between 2 and 3, an initial cooperator fraction

of $x_0 = 0.086$, and a regrouping time $T = 12 - 13$ h. Other model parameters were estimated as follows. The inherent fitness advantage of free-riders relative to cooperators was observed to be in the range between 1.04 and 1.05. In our model this translates to

$$f_C = 1, \quad (\text{S9})$$

$$f_D = 1.05, \quad (\text{S10})$$

where in contrast to equation (S3) we did not normalize the species related part, i.e. $\langle f \rangle \equiv 1$. The growth curves for different compositions of the population (see Fig.S3 in [1]) give access to the overall growth rate and its frequency dependence. From Fig.S3 in [1] we estimate:

$$r = 6.8 \times 10^{-4} \text{ min}^{-1}, \quad (\text{S11})$$

$$p = 6.6. \quad (\text{S12})$$

Employing these parameters in our model we have simulated the regrouping dynamics and find good agreement with the experimental results, cf. Fig. S3a. Since the population dynamics is still within the exponential growth phase at the regrouping time, we interpret the observed increase of cooperation as a group-growth mechanism. However, because of the particular set of experimental parameters, the resulting stationary cooperator fraction is very close to one which makes it difficult to observe coexistence between cooperators and free-riders. We can now use our theoretical model to explore the effects of an increase in the regrouping time. Changing the regrouping time from $T = 12.5$ h to $T = 375$ h we find that the time evolution of the cooperator fraction remains qualitatively similar, despite the fact that now cooperation increases because of the group-fixation mechanism, cf. Fig. S3b. Thus even by changing the regrouping time these small values of n_0 do not allow to distinguish between the two mechanisms. However, as discussed in the main text,

larger values of n_0 (in the range of 4 – 6) give a clear signature of each of the mechanisms upon varying the regrouping time.

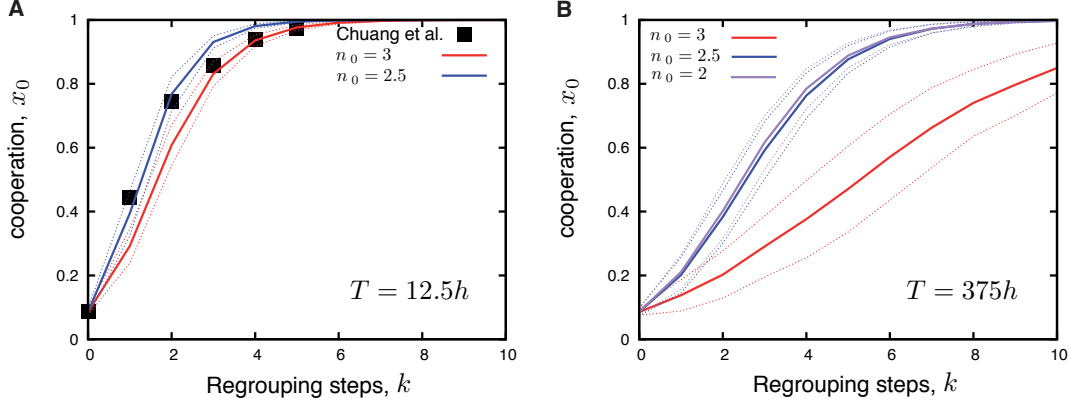


Figure S3: Increase in the level of cooperation for conditions resembling those examined by Chuang et al. [1]. **A** Short regrouping time, $T = 12.5h$. The measurements by Chuang et al. (black points) in comparison with the predictions of our model. Solid lines denote the expected level of cooperation. The dashed lines show the corresponding mean plus/minus the standard deviation. **B**, Large regrouping time $T = 375h$. For similar conditions, but a longer regrouping time, the outcome is qualitatively the same and only cooperators prevail. For both parts of the figure parameters are $x_0 = 0.086$, $r = 6.8 \times 10^{-4} \text{ min}^{-1}$, $f_C = 1$, $f_D = 1.05$, $p = 6.6$. In **A**, $K = 1.5 \times 10^6$. In **B**, $K = 1.5 \times 10^5$.

4 Captions of supporting videos

The two supplementary videos illustrate the group-growth and the group-fixation mechanism:

1. Video S1: Evolution of cooperation, caused by the group-growth mechanism
2. Video S2: Reaching purely cooperative behavior, caused by the group-fixation mechanism.

In detail, both videos show the probability distribution for groups of size N containing a fraction of cooperators, x and how it changes with time during the group evolution

step. The green dot indicates the mean fraction of cooperators. For several regrouping steps the evolutionary outcome depends strongly on the relative impact of the growth and fixation mechanisms. Here, this is exemplary shown for regrouping times $T = 2.5$, [video 1, group-growth mechanism dominates] and $T = 20$ [video 2, group-fixation mechanism dominates]. Parameters are given by $n_0 = 5$, $s = 0.1$, and $M = 5000$ for both videos.

4.1 Video S1

Small regrouping times (group-growth mechanism, see text): A single cooperating mutant can spread in the population. Starting from a very low initial fraction of cooperators, the level of cooperation increases during every regrouping step until a stable level of cooperation is reached. This behavior is caused by the faster growth of more cooperative groups as illustrated in the video by the strong correlation between the level of cooperation within a group and its speed of growth.

4.2 Video S2

Large regrouping times (group-fixation mechanism, see text): Above a certain threshold value in the level of cooperation, cooperators can overtake the entire population since purely cooperative groups are present and can play out their advantage in reaching a higher maximum group size even though all initially mixed groups are taken over by cheaters only.

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